RE-EVALUATION OF BRACT MORPHOLOGY IN TAXONOMY OF CORDYLANTHUS (SCROPHULARIACEAE)

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Cordylanthus taxonomy has traditionally relied heavily on the shape of the outer bract. One to several outer bracts are present at the base of each inflorescence, which in the species considered in the present study is reduced to a single flower (fig. 1 B and C) with one or two outer bracts. Of no concern here is the floral bract (fig. 1 B and D), which subtends each flower, resembles the ligulate calyx (fig. 1 E), and is remarkably uniform throughout most of *Cordylanthus*. The two existing treatments of the genus (Ferris, 1918; Pennell, 1951) use presence or absence of lobing of outer bracts as a character for separating species. During our comparative studies in the genus, we came to question whether this feature should receive such taxonomic weight. Entities that we judged to be closely related on the basis of a group of shared characters became widely separated taxonomically when outer bract shape, especially presence or absence of lateral lobing, was accorded overriding importance. We suspected that these bract variants might be interfertile and that the presence or absence of lobing of outer bracts is controlled by only small genic differences.

To test this hypothesis, two "species", showing general morphological similarity except for outer bract form, were artificially hybridized. *Cordylanthus brunneus* (Jeps.) Pennell, a fairly localized endemic of serpentine regions of Lake, Napa, and Sonoma Counties, California, has entire outer bracts (fig. 1 C). *Cordylanthus capillaris* Pennell (1950), known only from two populations in the Monte Rio-Occidental region in Sonoma County, about 40 km from the nearest population of *C. brunneus* and also on serpentine soil (see Bacigalupi, 1966), has bracts with one pair of lateral lobes (fig. 1 C).

These two species show other minor differences. Leaves as well as outer bracts of *C. brunneus* are narrowly linear while those of *C. capillaris* are filiform. The corolla of *C. brunneus* is mottled and striated with purplish maroon while in *C. capillaris* this coloration forms a solid band (fig. 1 F and G). In *C. brunneus* outer bracts and upper stems are sparsely glandular-puberulent while in *C. capillaris* they are glabrous. Lateral lobing of primary stem leaves, while not uncommon in *C. brunneus*, is a consistent feature in *C. capillaris* (fig. 1 A).

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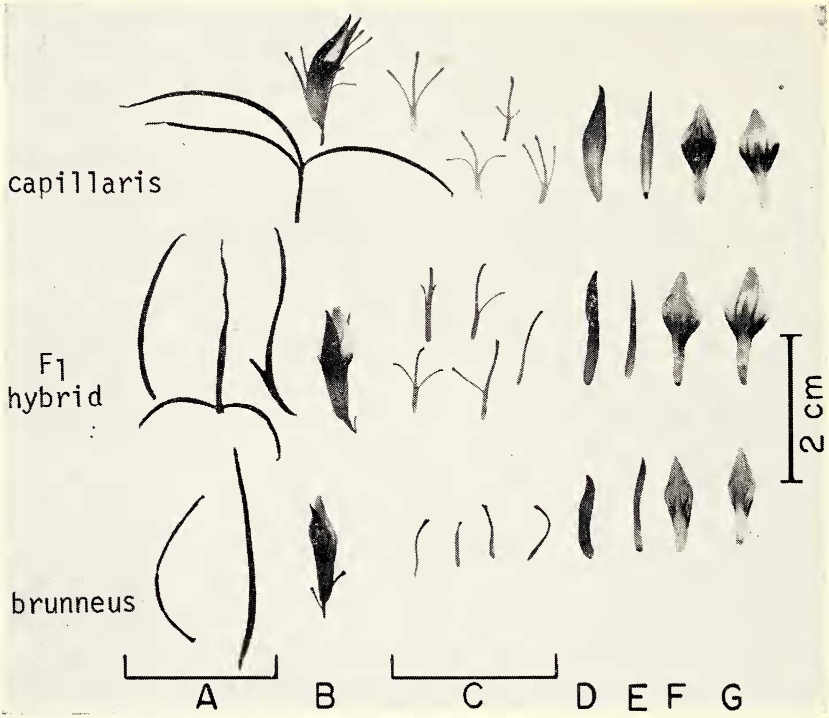

FIG. 1. Photographs of leaves, bracts, and flowers of *Cordylanthus brunneus*, *C. capillaris*, and their F_1 hybrid. Column A, leaf; B, single-flowered inflorescence with single floral bract, 1–2 outer bracts and 1 subtending bract; C, outer bracts; D, floral bract; E, calyx; F, dorsal view of corolla; G, ventral view of corolla.

METHODS

Parental strains were raised from seed obtained from type localities of each species. *Helianthus annuus* was used as host for these annual root hemi-parasites (Chuang and Heckard, 1971). Seed set is extremely rare on cultured plants lacking natural pollinators, although the plants are capable of some self-fertilization when artificially selfed. Higher seed set was obtained by crossing between different individuals. For this reason the F_2 generation was obtained by intercrossing F_1 plants rather than by selfing. One F_1 plant (number 3) was used as the female parent but pollen was taken indiscriminately from the other four F_1 plants. Likewise, the F_1 hybrids were obtained by using pollen from several plants of *C. capillaris* on the stigmas of one plant of *C. brunneus*. About 8–15 seeds per capsule are produced in nature but our artificial techniques yielded usually fewer than six seeds per capsule. Because of difficulty in making artificial hybridizations, the number of seeds produced per capsule is not believed to be a reliable criterion of interfertility. Estimates of fertility were made on pollen by examining ca 500 grains from at least three flowers per plant stained in lactophenol and cotton-blue.

Cytological preparations were made from aceto-carmine smears of microsporocytes preserved in a solution of chloroform: ethanol: glacial acetic acid (4:3:1, v/v).

Voucher specimens (JEPS and ISU) are as follows: *Cordylanthus brunneus* parent, Napa-Sonoma County line, N side of Mt. St. Helena, *Chuang 6843*; *C. capillaris* parent, Sonoma Co., 2.7 mi NE of Occidental, *Chuang 6845;* F_1 hybrids, *Heckard 71–7*; F_2 hybrids, *Heckard 72–31.*

RESULTS

Five plants of the F_1 generation were raised to maturity. Each had bract types of both parental plants in addition to an intermediate type with only one lateral lobe (fig. 1 C). Table 1 lists the number of these bract types for each of the five F_1 plants based on one count made towards the end of the flowering period. Usually there was only one outer bract per inflorescence (excluding the subtending bract of the inflorescence, which is similar to the upper leaves in lobing pattern). When occasionally two outer bracts were present, they were either the same or one was intermediate. Also listed for each F_1 plant is an estimate of pollen fertility as determined by pollen stainability. The average pollen fertility for the five F_1 plants was 75 percent, which can be compared with an average of 93 percent for the parents growing under similar conditions.

The 19 plants of the F_2 generation had a higher pollen fertility average, 91 percent, individual plants ranging from 85 to 98 percent. Some of the F_2 plants (Table 2) were like the parental types, with either entire or 2-lobed bracts, while others had combinations of two or three types. Rather than list the numbers of bract types in each of the F_2 plants, we have summarized the data to give the number of plants having each of the various bract conditions. It is perhaps noteworthy that of the six plants of the F_2 generation with all three bract types, five showed more inflorescences with the 2-lobed bract condition, whereas in the F_1 generation entire bracts outnumbered 2-lobed bracts.

Other characters mentioned earlier that show minor morphological differences between *C. brunneus* and *C. capillaris* were intermediate in

TABLE 1. DISTRIBUTION OF OUTER BRACT TYPES AND POLLEN FERTILITY IN FIVE PLANTS OF F_1 GENERATION OF CORDYLANTHUS BRUNNEUS–C. CAPILLARIS CROSS.

F_1 plant number	Bract condition			Pollen stainability
	entire	1 lateral lobe	2 lateral lobes	
1	113	18	21	78%
2	103	13	4	70%
3	151	114	89	80%
4	22	17	21	62%
5	180	82	70	82%

TABLE 2. SUMMARY OF OUTER BRACT LOBING IN 19 PLANTS OF F_2 GENERATION OF CORDYLANTHUS BRUNNEUS–C. CAPILLARIS CROSS.

Number of lateral lobes in bracts	Number of plants	Phenotypic summary
0 (as *C. brunneus*)	8	8 plants with entire bracts
0, 1, and 2	6	10 plants with intermediate conditions
0 and 1	2	
1 and 2	2	
2 (as *C. capillaris*)	1	1 plant with two lateral lobes

the F_1 plants, while intermediate and parental conditions appeared in the F_2 generation. No attempt was made to analyze inheritance of these features.

Chromosome numbers of $n = 14$ are reported here for the first time in both parents. No meiotic irregularity was seen in prophase and metaphase of the F_1 hybrids; normal segregation of 14 chromosomes occurred in anaphase.

DISCUSSION AND CONCLUSIONS

The high degree of interfertility between the bract-variants *"brunneus"* and *"capillaris"* and evidence that only minor genic differences control bract lobing indicate that these forms should be included in the same species. We will propose in our forthcoming taxonomic revision of subg. *Cordylanthus* that each variant be given subspecific status. Similarly, *C. viscidus* (Howell) Pennell of northern California and southern Oregon should be treated as conspecific with *C. tenuis* Gray of the Sierra Nevada, from which it differs largely in having lobed outer bracts. Likewise, *C. pilosus* Gray of the California Coast Ranges, with entire bracts, and *C. hansenii* (Ferris) Macbride of the Sierra Nevada foothills, with lobed bracts, are probably conspecific, as is suggested by the presence of intergrades (California, Shasta County, *Heckard 2799,* JEPS) in the region where their ranges juxtapose. These intergrades include individual plants with both bract types.

The small number of plants in the F_2 generation of the *C. brunneus -capillaris* cross did not allow analysis of the precise inheritance mechanism for bract shape. The segregation ratios of the F_2 plants [eight with entire bracts: ten intermediates: one 2-lobed (Table 2)] indicate that multiple genes may be operating with dominance for entire bracts. This is particularly suggested by the presence of only one plant with all 2-lobed bracts (as *capillaris*) and eight plants with entire bracts (as *brunneus*).

The F_1 plants that produced both parental bract types as well as intermediate forms are postulated to have genes that in the heterozygous condition were able to effect only partial expression of the dominant unlobed bract condition. The factors responsible for determining which particular lobing pattern develops in the embryonic stage are unknown.

The question of the origin of lobed bracts in the isolated southern populations *(C. capillaris)* merits consideration. The mutation producing lobing in outer bracts would seemingly not require a major change since the mechanism for producing a similar lobing in the leaves is already present in some plants of *C. brunneus*. Incorporation of this mutation into the population can be postulated to have come about by natural selection. However, the selective advantage of the lobed over the entire bract is not evident and a plausible alternative would be genetic drift or random fixation (Wright, 1931; Dobzhansky, 1941) of non-adaptive features. The necessary prerequisites for random fixation in plants, as discussed by Stebbins (1950), could have been present in this case: a small, isolated population confined to open barrens of a small serpentine "island". If genes for lobed bracts arose by mutation in such a population, this feature could become established by chance survival of mutant types during a period of severe stress when the population was highly reduced and only seed of the mutant survived. Reduction in population size to zero or nearly so does occur in the genus, as was observed in *C. helleri* (Ferris) Macbride of the western Great Basin when seed germination was reduced apparently by drought (Chuang and Heckard, 1971).

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LITERATURE CITED

BACIGALUPI, R. 1966. A correction for the type locality of *Cordylanthus capillaris* Penn. Leafl. W. Bot. 10:287–288.

CHUANG, T. I. and L. R. HECKARD. 1971. Observations on root-parasitism in *Cordylanthus* (Scrophulariaceae). Amer. J. Bot. 58:218–228.

DOBZHANSKY, T. 1941. Genetics and the origin of species. Columbia Univ. Press, New York.

FERRIS, R. S. 1918 Taxonomy and distribution of *Adenostegia*. Bull. Torrey Bot. Club 45:399–423.

PENNELL, F. W. 1950. *Cordylanthus capillaris,* a new bird's beak (Scrophulariaceae) from California. Notul. Nat. Acad. Sci. Philadelphia 223:1–2.

————. 1951. Scrophulariaceae. *In* L. Abrams, Illustrated flora of the Pacific States 3:686–859. Stanford Univ. Press, Stanford.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.